

THE FAMILY HIMANTANDRACEAE

I. W. BAILEY, CHARLOTTE G. NAST, AND A. C. SMITH

With six plates

THE present paper is the second of a proposed series discussing the interrelationships of the families of woody Ranales. We have already briefly discussed the position of the Himantandraceae as a relative of the Magnoliaceae and the Degeneriaceae (1). These three families form a compact group within the Ranales, being more closely related to each other, on the basis of important morphological details, than any one of them is to other families.

The most important contributions to our knowledge of the Himantandraceae were made by Diels (3, 4, 5), with whose conclusions (5: 134) that the closest relative of the group is the Magnoliaceae we are in essential agreement. Diels has discussed *Himantandra* in considerable detail, and therefore we shall emphasize those points which he was unable fully to observe, and especially those characteristics of *Himantandra* which we interpret differently.

The first part of this paper presents a diagnosis of the technical characters of *Himantandra*, the sole genus of the family, and the two known species. Only the essential citations to literature are given, as fuller citations were recently listed (7) and the status of the generic name was discussed. In the second part of this paper we shall examine the internal morphological features of the genus, with special reference to points not made entirely clear by Diels. Specimens cited in this treatment are deposited in the herbarium of the Arnold Arboretum. The morphological and anatomical portions of this study have been prepared by the first two authors, the taxonomic portion by the third author, while the conclusions are the result of collaborative discussions.

I

Himantandra F. v. Muell. Pap. Pl. **2**: 54. 1890.

Galbulimima F. M. Bailey in Queensl. Dept. Agr. Bot. Bull. **9**: 5. 1894.

Trees, the branchlets slender, subterete or faintly angled distally, densely lepidote; scales covering the young branchlets, petioles, lower surface of leaf-blades, and external parts of inflorescence (except stamens and staminodes), these scales peltate, membranaceous, castaneous, dark at center, paler toward margin, the stalk very minute, the body composed of 30–56 radiating flattened laterally coalescent hairs; stipules none; leaves alternate, simple, pinnate-nerved; petioles slender, rugulose; leaf-blades coriaceous or thin-coriaceous, entire and faintly recurved or plane at margin, the costa prominent beneath, the secondary nerves 7–16 per side (interspersed

with other similar but weaker or obscure laterals), spreading, anastomosing toward margin (either freely or obscurely so); flowering shoots axillary, customarily with 1 terminal flower, with 2 (sometimes 3) alternating bracts, the bracts subcoriaceous, oblong, 1–3 mm. long, occasionally foliaceous, with obscure axillary buds, these buds rarely developing into subsidiary flowering axes with two scales and an apical flower; pedicel similar to the flowering shoot in texture; calyx subcoriaceous, ovoid-conical, obtuse or umbonate at apex, calyptrate, rupturing along an irregular line near base and leaving a small undulate or irregularly lobed calycine remnant attached to the torus, glabrous within, densely and uniformly lepidote without; corolla similar to calyx in texture, shape, and indument, slightly smaller than and closely enveloped by the calyx, similarly calyptrate; torus carnose, flaring to the attachment of the calyx and corolla, thence columnar and copiously staminiferous, concave on the distal surface and giving rise to a conical carpel-bearing apex; outer staminodes about 7–23, 1- or 2-seriate, castaneous, carnose, sharply reflexed after anthesis; stamens numerous, several-seriate, closely appressed, similar to outer staminodes in texture and shape, rapidly elongating and reflexed after dehiscence of the perianth, the pollen-sacs 4, paired, extrorse, immersed in the sporophyll-tissue, linear, obtuse at base and apex, dehiscing longitudinally; inner staminodes about 13–20, 1–3-seriate, similar in texture to the outer staminodes, linear-subulate, gradually narrowed to an acute apex, usually erect and more or less coherent at base; carpels spirally arranged on the conical apical portion of the torus, free but laterally appressed and soon concrescent, the ovary ovoid or oblong-ellipsoid, densely lepidote on the thick outer surface, glabrous on the thinner lateral surfaces, gradually narrowed distally into a subulate style, the styles plume-like, soft and glandular in texture, sometimes cohering in a gelatinous mass, the locule 1, the ovule 1 (rarely 2, but the second seldom developing), anatropous, attached to the ventral margin at various levels in different carpels; fruit an ellipsoid or subglobose syncarp, up to 25 mm. in diameter at maturity, rounded or obtuse at base and apex, the pericarp coriaceous, 0.5–1.5 mm. thick, red, rugulose when dried, lepidote without, the scales long persistent, the carpels completely coalesced, often imbricate and superposed in 2 or 3 ranks, the exterior ones appearing shorter than the interior, the dissepiments coriaceous, persistent, the endocarp cartilaginous, the seeds solitary (or possibly rarely 2), with oily endosperm and small embryo near the hilum.

KEY TO THE SPECIES

- Leaf-blades usually oblong-elliptic, (6–)7–15 cm. long, (3–)4–7 cm. broad (2–2.5 times as long as broad), obtuse to acute at base, rounded to acute at apex; scales on lower surface of mature leaf-blades 0.15–0.4 mm. in diameter, crowded, usually completely obscuring the surface, the margins of adjacent scales often imbricate, at least contiguous, only rarely not touching; outer staminodes about 12–23; stamens 90–130, 6–25 mm. long; inner staminodes 15–20; carpels 9–15; New Guinea (and probably North Moluccas). 1. *H. Belgraveana*.
- Leaf-blades oblong-lanceolate, 7–11.5 cm. long, 2–4 cm. broad (about 3 times longer than broad), acute to attenuate at base, subacute to short-acuminate at apex; scales on lower surface of mature leaf-blades 0.13–0.17 mm. in diameter, comparatively scattered, the margins of adjacent scales not imbricate, rarely contiguous; outer staminodes about 7; stamens about 40, 6–9 mm. long; inner staminodes about 13; carpels 7–10; Queensland. 2. *H. baccata*.

1. **Himantandra Belgraveana** (F. v. Muell.) F. v. Muell. Pap. Pl. **2**: 54. 1890.
Eupomatia Belgraveana F. v. Muell. in Austral. Jour. Pharm. **2**: 4. 1887, in Bot. Centralbl. **30**: 325. 1887.
Galbulimima Belgraveana Sprague in Jour. Bot. **60**: 138. 1922.
Himantandra nitida Bak. f. & Norman in Jour. Bot. **61**: Suppl. 2. 1923.
Galbulimima nitida Sprague in Jour. Bot. **61**: 200. 1923.

Tall tree, up to 25 m. or more high; branchlets straight or subflexuose, 2–4 mm. in diameter toward apices, pale brown or castaneous or at length fusco-cinereous; scales 0.15–0.4 mm. in diameter, crowded, usually completely obscuring the surface, the margins of adjacent scales often imbricate; petioles 1–2 mm. in diameter, 8–24 mm. long, deeply or shallowly canaliculate; leaf-blades coriaceous, brown or dark olivaceous, smooth or densely and minutely papillose, and shining or dull above when dried, castaneous- or fuscous-lepidote beneath, oblong (rarely ovate- or obovate-) elliptic, (6–)7–15 cm. long, (3–)4–7 cm. broad, obtuse to acute at base, rounded to acute and sometimes inconspicuously mucronulate at apex, the costa impressed or deeply canaliculate above, the secondary nerves 8–16 per side, straight, sharply raised or prominulous or immersed above, faintly prominulous or immersed beneath, the veinlets immersed, occasionally forming a faintly prominulous reticulum above and rarely beneath; flowering shoots 1.5–6 cm. long inclusive of flower or fruit, the vegetative portion slender, rugulose, 1–2 mm. in diameter, up to 25 mm. long, the pedicel gradually swollen distally to 3 mm. in diameter, 8–16 mm. long at anthesis, up to 20 mm. long in fruit; calyx 9–16 mm. long and 8–13 mm. in diameter at anthesis; outer staminodes about 12–23, 1- or 2-seriate, oblong-ligulate, 5–11 mm. long at anthesis and probably often longer, 1.5–2 mm. broad near base, gradually narrowed to a sharp and often unequally apiculate or rostrate apex, sometimes sparsely pellucid-glandular; stamens 90–130, usually 6- or 7-seriate, 6–25 mm. long, 1.5–2 mm. broad near base, often with numerous and obvious sclereids and obscurely or obviously striate, the pollen-sacs 0.8–1.8 mm. long, the lower edge 0.6–3 mm. distant from the base of the sporophyll; inner staminodes 15–20, 1–3-seriate, 5–7 mm. long, 0.5–1.3 mm. broad near base; carpels 9–15, 4–6 mm. long at anthesis, the ovary 1.5–2 mm. long; fruit with seeds (in all our specimens) solitary, flattened, submembranaceous, suborbicular, 3–4 mm. in diameter, apparently sterile.

DISTRIBUTION: New Guinea, and probably also some of the islands to the west. Diels (5: 131) reports that Warburg (no. 17770) collected loose flowers which are probably referable to the species at Sibela, on Batjan, an island south of Halmahera; extension of typical New Guinean elements to this region is frequent.

NETHERLANDS NEW GUINEA: Biak I., Seroei, alt. about 50 m., *Neth. Ind. For. Serv.* 30722, 30898; Japen I., Seroei, alt. about 370 m., *Neth. Ind. For. Serv.* 30406; 6–15 km. southwest of Bernhard Camp, Idenburg River, alt. 1300–1800 m., *Brass & Versteegh* 11195 (tree 25 m. high, frequent in primary forest on slopes of a ridge, the trunk 34 cm. diam., the crown not wide-spreading; bark 5 mm. thick, dark brown, fairly smooth; wood white; fruits red), *Brass* 12103 (tree to 25 m. high, abundant in mossy-forest; flowers white; fruits orange-brown), *Brass & Versteegh* 12572 (tree 21 m. high, occasional in primary forest on slopes of a ridge, the trunk 51 cm. diam., the crown fairly small; bark 9 mm. thick, gray, smooth; wood light brown; flowers yellow; fruits green). NORTHEASTERN NEW GUINEA: Sepik River region, Hauptlager Malu, alt. 50–100 m., *Ledermann* 10884a (frag.); Morobe District: Yunzaing, alt. 1200–1350 m., *Clemens* 3586, 3678, 6498, 6503 (large trees, the trunk to 1 m. diam.; fruit red); Ogeramngang, alt. 1750–1800 m., *Clemens* 4991, 5538; between

Ogeramnang and Tobou, alt. 1500–1800 m., *Clemens 6584a*; Matap, alt. 1500–1800 m., *Clemens 11100, 41200* (tall trees; “inflorescence” brown; flowers russet-green). BRITISH NEW GUINEA: Central Division, Mt. Tafa, alt. 2400 m., *Brass 4916* (tall tree, plentiful in valley forests, with slender trunk and thinly foliated crown; staminodes and stamens cream-colored; fruit brown).

In studying the above-cited specimens, we have noted certain differences which we have tried to correlate with the different geographic areas, thinking that more than one nomenclatural division of the genus might be discernible in New Guinea. However, our attempts to divide the New Guinean population have not succeeded, and we have reached the conclusion that only one species is represented.

The material from the Morobe District has the upper surface of the leaves usually dull and conspicuously rugulose-papillose, while the remaining collections have this surface comparatively shining and essentially smooth. However, there are exceptions to this generalization, and the texture of the upper surface appears to be subject to individual variation, possibly being dependent upon the size and distribution of stone-cells. The degree to which the secondary nerves are immersed is also subject to great individual variation, although in general the Morobe collections have more completely immersed nerves. When young, the leaves are infolded with the two halves of the upper surface closely appressed. Although mature leaves are always strictly glabrous on the upper surface, these young folded leaves sometimes bear small many-branched stellate hairs before they open. Such hairs are often found in material from the Morobe District, but they are apparently always lacking in the other specimens cited.

On the basis of size and number of floral parts, no important differences are found among the available collections, the species being very variable in this respect. The greatest variability is found in the size of the stamens and outer staminodes, which elongate rapidly after the dehiscence of the corolla. The longest stamens we have observed are 18 mm. long, but Diels (4) portrays the stamens of the type collection as about 25 mm. long, and we have no reason to doubt the accuracy of this observation.

From our study of the available material and the earlier descriptions, therefore, we are inclined to believe that *Himantandra* is represented in New Guinea by only one species.

Himantandra Belgraveana has as its type a specimen collected by Forbes (no. 759 according to Mueller, no. 795 according to Diels [4] and Baker [2]), collected in the vicinity of Sogere, British New Guinea. The original description does not give dimensions, but Diels' description in 1912 (4) is adequate. *Himantandra nitida* is based upon *Forbes 828a* from the same region; according to Baker and Norman this differs from the earlier species “by the shining broader coriaceous leaves and much longer stamens.” A comparison of the description of *H. nitida* with our concept of *H. Belgraveana* does not demonstrate differences of any consequence.

2. ***Himantandra baccata*** (F. M. Bailey) Diels in Bot. Jahrb. **55**: 128. 1917.

Galbulimima baccata F. M. Bailey in Queensl. Dept. Agr. Bot. Bull. **9**: 5. 1894.

Tree up to 17 m. high, the branchlets 1.5–3 mm. in diameter toward

apices, brownish; scales 0.13–0.17 mm. in diameter, comparatively scattered, the margins of adjacent scales not imbricate, rarely contiguous; petioles 0.7–1 mm. in diameter, 8–20 mm. long, shallowly canaliculate; leaf-blades thin-coriaceous, dark brown and shining above when dried, castaneous-lepidote beneath, oblong-lanceolate, 7–11.5 cm. long, 2–4 cm. broad, acute to attenuate at base, subacute to short-acuminate at apex, the costa shallowly impressed or slightly raised above, the secondary nerves 7–10 per side, prominulous above, less conspicuously so beneath, the veinlets immersed or faintly prominulous above; flowering shoots up to 2 cm. long at anthesis, the vegetative portion angled, 5–13 mm. long, the pedicel shorter; calyx up to 10 mm. long and slightly less in diameter at anthesis; outer staminodes about 7, 1-seriate, lanceolate, 4–6 mm. long or probably longer after anthesis, acute; stamens about 40, several-seriate, 6–9 mm. long, the pollen-sacs 1.5–2 mm. long; inner staminodes about 13, 6–8 mm. long, narrowed at base; carpels 7–10, about 2 mm. long at anthesis; fruit with seeds “with a loose outer ragged coat; testa smooth, cartilaginous; albumen copious, oily. Embryo not particularly small near the hilum, apical with reference to the position of the seed in the berry.” (ex F. M. Bailey).

DISTRIBUTION: Queensland, Australia.

AUSTRALIA: Queensland: North Queensland, Gadgarra, Pearamon, Atherton, *White 1561*. In addition to the preceding specimen, which is the only one we have seen, the following are cited by other writers, all from Queensland: Eumundi, *Arundell* (TYPE); Boar Pocket and Evelyn, Heberton District, *J. F. Bailey*; Kin Kin, North Coast Line, *Francis*.

Our description is based primarily upon the White collection, which is in fruit; we have also incorporated the characters and dimensions recorded by F. M. Bailey and Sprague (see Smith [7] for citations).

INADEQUATELY KNOWN SPECIES

HIMANTANDRA PARVIFOLIA Bak. f. & Norman in Jour. Bot. **61**: Suppl. 2. 1923.

Galbulimima parvifolia Sprague in Jour. Bot. **61**: 200. 1923.

This species, known to us only from the original description, is based on *Forbes 355*, from Meroka, British New Guinea. The leaves described seem closer to those of *H. baccata* than to those of *H. Belgraveana*, but they are even smaller than any described for *H. baccata*, being similar in proportions. The species is said to differ from *H. baccata* in its smaller leaves and flowers, but the dimensions given for the flowers do not indicate this to be the case. No numbers of floral parts are given.

From the locality, one would expect this to be a depauperate form of *H. Belgraveana*, but the leaf-proportions do not suggest this. If it represents *H. baccata*, the occurrence of this species in New Guinea will be noteworthy. *Himantandra parvifolia* may quite possibly be a good third species of the genus, but for the time being we are inclined to believe it an extreme variation of *H. Belgraveana*, which, as illustrated by the specimens cited above, seems best interpreted as a very variable species.

II

As indicated above, we are much better acquainted with the New

Guinean species than with the Australian, and consequently the following notes are based primarily upon *H. Belgraveana*, of which we have ample recently collected material. The Australian species and *H. Belgraveana* are very closely related and show only minor differences, and for this reason we do not doubt that remarks on the morphology of one species apply equally well to the other.

STEM. In *Himantandra baccata* and *H. Belgraveana*, as in *Degeneria* and the Magnoliaceae,¹ the primary vascular cylinder is a dictyostele, being constituted of discrete bundles that are separated by relatively wide gaps. Each bundle is capped externally by slender thick-walled fibers and is subtended internally by vertically elongated, thin-walled parenchyma. During the earlier stages of the formation of the secondary body, the external arcs of fibers tend to become united into a continuous ring of sclerenchyma by the sclerification of the intervening arcs of parenchyma. The bulk of the pith is composed of large comparatively thin-walled cells, but nests and transversely oriented plates of sclereids are of common occurrence, particularly in the nodal parts of the stem. The cortex is characterized by having numerous spherical secretory cells and more or less abundant sclereids. Crystalliferous parenchyma occurs in the cortex, phloem, and pith, usually in close association with the sclerenchyma. Each small crystal-bearing cell or chamber contains a single rhombohedral crystal of calcium oxalate that is jacketed by a thick sheath of lignified cellulose. As noted by Diels (5), the origin of the cork is superficial, probably hypodermal.

The rays of the first-formed secondary xylem are narrow, with a high ratio of uniseriate to biseriate, and are markedly heterogeneous. On the contrary, in wood from large stems (*fig. 10*), there is a high ratio of fusiform, nearly homogeneous triseriate and tetraseriate rays, and uniseriate rays are much reduced in size and number. The vessels of the first-formed secondary xylem are smaller, more numerous, and occur in more extensive radial seriations than they do in the later-formed wood (*fig. 9*). Furthermore, the vessels of the metaxylem and of the first-formed secondary xylem commonly exhibit a higher ratio of scalariform to porous perforations and of scalariform and opposite to alternate lateral pitting than do the vessels of the later-formed wood, where scalariform perforations and transitional types of lateral pitting are evanescent or vestigial. It should be noted in this connection that the discrepancies in Diels' (5) and McLaughlin's (6) descriptions of the wood of *Himantandra* may have been due in part to differences in the type of material examined by them. The wood fibers of *Himantandra* are comparatively thin-walled fiber tracheids, having small circular bordered pits. The wood parenchyma is of a broad banded apotracheal type (*fig. 9*). More or less numerous strands of crystal-bearing cells occur in association with the wood parenchyma.

¹Whenever mentioned in the following pages, the family Magnoliaceae is intended in the restricted sense of Dandy, Hutchinson, and others, viz. exclusive of the Winteraceae, *Illicium*, Schizandraceae, and *Tetracentron*.

In herbarium specimens of *Himantandra*, there is less conspicuous flaring of the rays in the secondary phloem than in comparable material of *Degeneria* and of most Magnoliaceae, and stratified hard and soft bast are less precociously developed. It is significant, however, that in larger stems the phloem is distinctly stratified and has flaring rays. Furthermore, the sieve tubes are of the same structural type as in the Magnoliaceae and *Degeneria*. Crystalliferous parenchyma occurs along the surfaces of the hard bast.

LEAF AND NODAL ANATOMY. In *Himantandra Belgraveana* and *H. baccata*, three traces enter the base of the petiole, leaving three gaps in the cauline vascular cylinder, i. e. the stems have typically *trilacunar* nodes. The three traces divide forming 6–8 vascular bundles that become oriented into a more or less cylindrical foliar dictyostele (*fig. 8*). As in *Degeneria* and the Magnoliaceae, the vascular strands that branch outward from the median trace are segregated in opposite sides of the foliar dictyostele. In other words, one or more of them retain a normal orientation of xylem and phloem and form part of the abaxial surface of the foliar stele, whereas the remaining ones develop an inverted orientation of xylem and phloem and form part of the adaxial surface of the foliar vascular cylinder. Thus, the vascularization of the petiole and midrib is of a fundamentally different type than that which occurs in such ranalian plants as *Tetracentron*, where a medullated foliar dictyostele is formed by the closure of an adaxially expanding arc of vascular tissue.

The young leaves of *Himantandra* are adaxially folded, i. e. conduplicate (*fig. 3*). They do not unfold until they have attained a considerable size, not infrequently a length of 8 centimeters or more in the case of the larger-leaved specimens. The exposed abaxial surfaces of the conduplicate leaves, from very early stages of their development, are provided with a dense coating of peltate scales (*fig. 3*). These scales are persistent on the unfolded mature leaves (*fig. 1*), but are smaller and less crowded in *H. baccata* than in *H. Belgraveana*. The adaxial or upper surfaces of mature leaves of all investigated specimens of *Himantandra* are glabrous, but the immature leaves of certain collections of *H. Belgraveana*, viz. *Clemens 3586, 3678, 4991, 5538, 6498, 6503, and 6584a*, bears scales or stellate hairs on their ventral surface during certain stages of their conduplicate development. The ray cells of these scales or stellate hairs are not firmly coherent and drop off during subsequent development of the leaf. However, the basal cells or stalks are persistent and are more or less widely scattered among the epidermal cells of the upper surface of the mature leaf.

The stomata of both *H. baccata* and *H. Belgraveana* have a very peculiar and highly characteristic distribution. As shown in *fig. 2*, they occur in discrete, nearly circular clusters that subtend each of the peltate scales on the lower surface of the leaf. Crystal-bearing cells, of the same morphological type as in the stem, are more or less abundant in the leaf. They tend to occur characteristically in pairs or small clusters in the lower epidermis (*fig. 1*), and in strands along the sclerenchymatous sheaths of the

veins and veinlets. Numerous clusters or nests of sclereids are scattered throughout the mesophyll of all the Clemens collections of *H. Belgraveana*, but they are absent or of less frequent occurrence in other material examined by us. Spherical secretory cells are abundantly developed in the leaf, as in the other organs of the plant.

FLOWERING SHOOTS. The solitary bisexual flowers of *Himantandra*, as of *Degeneria* and certain genera of the Magnoliaceae, e. g. *Michelia* and *Elmerrillia*, are borne at the apex of axillary shoots. These flowering axillary shoots are provided with two (occasionally three) scales which have more or less rudimentary buds in their axils. Since the scales frequently develop into typical leaves, they may be interpreted as reduced foliar organs. In exceptional instances, one of the buds develops a subsidiary flowering axis bearing two scales and an apical flower. The flowers are separated from the upper scale or leaf by an internode of considerable length, which may be designated as the pedicel in contrast to the essentially vegetative nodes and internodes that subtend it. The pedicel flares toward the base of the torus, forming a circular flange (*figs. 11, 12*), to which the calyptrate calyx is attached. A second internal flange provides an attachment for the calyptrate corolla. The carpel-bearing, cone-like apex of the torus (*fig. 12*) projects from the concave upper surface of the broadly columnar part of the receptacle, to which the stamens and staminodes are attached.

The axillary flowering shoot contains a dictyostele of many small bundles (*figs. 15-18*) similar to that of a typical vegetative branch, except for a short distance in the basal part of the pedicel. Here the bundles are constricted into four large vascular strands (*fig. 17*). Three traces (*figs. 15, 16*) enter¹ the first bract, leaving three gaps in the stele, just as in the case of the leaves of ordinary vegetative shoots. The three traces of the second bract (or leaf) initiate their departure at a slightly higher level and from the opposite half of the stele. Although these traces fluctuate considerably in their subsequent behavior, two of them (commonly the median and one lateral) tend to divide, forming two additional traces that extend upward through the cortex of the pedicel (*figs. 15-18*). A third set of three traces departs from the stele just above the level of the first node (*fig. 16*). These traces are detached from the same half of the stele as the three traces of the first scale and extend upward through the cortex of the second internode, the second node, and the pedicel (*figs. 16-18*). Thus, there are five cortical bundles in the base of the pedicel, to which is soon added a sixth bundle which departs from the same side of the stele as the median trace of the second scale (*figs. 16, 17*). As will be shown subsequently, these six cortical bundles of the pedicel vascularize the outer calyptra.

Since the foliar appendages of *Himantandra* have a $\frac{1}{2}$ phyllotaxy and are attached to trilacunar nodes, it is evident that the flowering shoot and

¹The terminology used is purely descriptive and bears no ontogenetic implications regarding downward or upward development of procambium, phloem, and xylem.

pedicel have four distinct sets of three traces, each set attached alternately to opposite sides of the stele. The lateral traces of the fourth set exhibit more or less conspicuous fusion to the traces of the second set. Therefore, the outer calyptra of the flower represents a pair of fused appendages, either bracts or sepals. It should be emphasized in this connection, however, that if the homologous appendages of *Degeneria* are typical sepals, the outer calyptra of *Himantandra* should similarly be designated as calyx. Furthermore, the calyptrate calyx of *Drimys* is obviously composed of two fused sepals.

The vascularization of the torus is extremely complex and variable. There is a network of variously oriented bundles which divide, anastomose, redivide, reanastomose, and shift position throughout the torus. The number and arrangement of the bundles varies to a certain extent in different flowers, indicating a lack of stabilization within the genus. A basic or average condition is, therefore, illustrated in *figs. 18-23*. The six cortical bundles of the pedicel (*fig. 18*) either bifurcate or break up into several branches (*fig. 19*). These branches divide laterally into smaller strands (*fig. 20*) and internally into strands which extend upward through the base of the torus (*fig. 21*). The lateral strands may divide or anastomose in the base of the outer calyptra, but eventually they enter its free part as numerous small strands variable in size and number (*fig. 21*). The internally directed branches are usually eight in number, exhibiting considerable diversity in their relations to the branches of the six cortical bundles of the pedicels. For example, cortical bundle no. 1 in *figs. 18-20* bifurcates laterally, one branch of which forms an internal strand. Cortical bundle no. 2 divides laterally and produces two internally directed strands, whereas cortical bundle no. 3 gives rise to no internal strands. To these eight peripheral strands, four additional strands are added from the central stele (blackened strands of *figs. 19-21*), making an outer ring of twelve strands in the part of the torus subtending the inner calyptra (*fig. 21*). These twelve bundles divide laterally (*fig. 22*), and some of them may be joined by a few tracheal elements to an average of five smaller internal bundles (unstippled strands of *figs. 20-22*) which depart from the stele at a higher level than the four bundles referred to above. The five smaller internal strands, however, are only feebly and temporarily attached to the vascular system of the inner calyptra and subsequently extend upward through the torus (*fig. 23*). The lateral branches of the twelve bundles of the inner calyptra divide and anastomose laterally, giving rise to an indefinite number of small strands which enter the free part of the inner calyptra (*fig. 23*). Simultaneously with the lateral divisions, a few internally and upwardly directed branches are formed. Thus, at the bases of both the outer and the inner calyptras, a certain amount of vascular tissue remains in the torus to become traces or parts of traces for the succeeding appendages.

The basic pattern in the vascularization of the inner calyptra evidently consists of four sets of three traces. There are apparently four median

traces that are attached to the central dictyostele and four pairs of lateral traces that are joined to the cortical system of calycine bundles. Such an interpretation is strengthened by comparisons with the flowering axis of *Magnolia*, *Liriodendron*, and other Magnoliaceae, where complex systems of cortical bundles are characteristically present. In these magnoliaceous plants, the dorsal trace of the 3-veined carpels is attached to the central dictyostele, whereas the two lateral traces tie into the cortical system of vascular bundles. This indicates that the inner calyptra of *Himantandra* is composed of four fused appendages, and comparisons with homologous members of *Degeneria* demonstrate that it is a corolla. We are unable to follow Diels (5) in homologizing the calyptras of *Himantandra* with the bud-scales of *Michelia Figo* (Lour.) Spreng., since the scales of both vegetative buds and flower-buds are clearly of stipular origin in the Magnoliaceae.

In a former comparison between the floral axes of Degeneriaceae, Magnoliaceae, and Himantandraceae (Bailey and Smith, 1), we failed to recognize fully the vascular complexities of *Himantandra*. Subsequent detailed investigations of more abundant and adequate material have shown that this genus resembles the Magnoliaceae rather than *Degeneria*, although its vascular complexities appear to be less stereotyped and stable than in many Magnoliaceae. The flowering shoots and pedicels of *Degeneria* do not have complicating systems of cortical bundles.

STAMENS AND STAMINODES. The columnar region of the torus upon which the stamens and staminodes are borne contains the terminus of the increasingly complex network of vascular strands. The strands in this region of the torus comprise (1) upward extensions of the inwardly directed branches of the corollaceous vascularization (*figs. 22, 23*), (2) upward extensions of the bundles which become temporarily attached to this system, and (3) additional traces detached from the central dictyostele, which loses its identity as a cylinder by the branching, rebranching, and dispersal of its constituent bundles. Traces from the strands in the peripheral regions vascularize the outer staminodes and lower stamens. The upper stamens and inner staminodes have traces that arise from the dispersed bundles of the dictyostele. Three traces from three separate strands enter the base of each fertile microsporophyll and likewise a majority of the sterile ones. In the case of the broad outermost staminodes and the innermost awl-shaped ones, the traces are sometimes reduced to two or one.

The stamens of *Himantandra* are not differentiated into filament, anther, and connective, and are best described as much elongated, narrowly lanceolate sporophylls (*fig. 25*). This was recognized by Diels, who states (5: 129): "Es ist unangebracht, bei diesen Sporophyllen überhaupt von Konnektiv oder Anthere zu reden. Denn der Blattcharakter ist kaum gestört, . . ." Each microsporophyll bears two pairs of vertically elongated sporangia that are immersed beneath the abaxial surface of the sporophyll. Dehiscence is longitudinal and extrorse. In transverse sections cut at the level of the sporangia (*fig. 5*), the microsporophylls of *Himantandra* exhibit

close similarities to those of *Degeneria*, not only as regards their general topographical features, but also concerning specific peculiarities of their endothecia. Three veins enter the base of the microsporophylls as in *Degeneria*, but there is more extensive branching of the veins in the sporophylls of the Himantandraceae than in the much shorter microsporophylls of the Degeneriaceae. Although the details of the vascularization fluctuate considerably from flower to flower of different collections and from stamen to stamen of the same flower, the marginal veins rarely extend beyond the lower third of the sporophylls of *Himantandra* (fig. 25) and tend to anastomose with the median vein or its branches just above the level of the sporangia. The paired sporangia are situated between the median and marginal veins and thus, as in *Degeneria*, cannot be regarded as slightly displaced marginal, or terminal, structures. Furthermore, in the Himantandraceae, as in the Degeneriaceae, the veins and veinlets are not directed toward the sporangia and do not establish connections with the endothecia.

The staminodes of *Himantandra* resemble the microsporophylls in general form and texture (figs. 24, 26), but their median and lateral veins commonly exhibit less extensive branching. Furthermore, in the outermost broad sterile sporophylls and the innermost awl-shaped ones, the lateral veins frequently are much reduced in length or are absent. The sterile sporophylls resemble the fertile ones in having numerous spherical secretory cells, more or less abundant nests of sclereids, and in being devoid of peltate scales, which are such characteristic features of the other organs of the plant.

The occurrence of staminodes within the fertile microsporophylls has been noted in *Degeneria*, which, like *Himantandra*, differs from the Magnoliaceae in this respect (Bailey and Smith, 1). The fact that in *Himantandra* sterile microsporophylls occur outside, as well as inside, the fertile ones does not appear to be of great significance, as in all respects except their sterility these staminodes are similar to the stamens. To interpret the outer staminodes as petals, Sprague (7) seems to have no justification. Therefore, we are in agreement with Diels (5: 129) in interpreting these outer appendages as sterile microsporophylls.

The pollen of *Himantandra* is provided with a single germinal furrow and therefore is of the monocolpate type. As in the Magnoliaceae, the form and the dimensions of the pollen fluctuate during expansion and contraction of the grains. When fully expanded the pollen tends to be nearly spherical, with diameters of from 30 to 38 microns. As the tenuous floor of the furrow invaginates during contraction, the grains become ellipsoidal, whereas when it evaginates the outlines of the grains become triangular in certain planes of orientation. The exine is thin and comparatively homogeneous, but, as in the case of many of the so-called smooth exines of Magnoliaceae, it exhibits minute pits or granulations when examined under high magnification in lactic acid.

CARPELS. The young carpels, like the young leaves, of *Himantandra*

are adaxially folded, viz. conduplicate, but the margins and the ventral surfaces of the free parts of the carpels (*fig. 6*) commonly are less closely approximated than those of the immature leaves (*fig. 3*). The adaxially oriented margins at the base of the carpels are adnate to the cone-shaped apex of the torus (*fig. 7*). At this level of the floral axis, there is more or less lateral concrescence of carpels, a tendency which becomes markedly intensified during the development of the fruits. The free parts of the carpels between the level of adnation and the base of the style not infrequently remain open at anthesis (*fig. 4*). The glandular cells of the plume-like style (*figs. 13, 14*) extend downward along the free margins and adjacent ventral surfaces of the carpel to the level of attachment of the large, much flattened, anatropous ovule. A transverse section of this free open part of the carpel (*fig. 4*) resembles a transverse section of the megasporophyll of *Degeneria* except that the ovule is attached closer to the margins of the conduplicate carpels than are the numerous ovules of *Degeneria*. In the Degeneriaceae, one is concerned with a seemingly primitive, conduplicate, 3-veined megasporophyll of comparatively unmodified form, bearing numerous ovules on its adaxial or ventral surface and having stigmatic structures along its margins and adjacent parts of its free ventral surfaces. With the reduction in the number of ovules to a single one (rarely two) in *Himantandra*, there appears to have been a concomitant narrowing of the sterilized upper $\frac{3}{5}$ to $\frac{5}{7}$ of the megasporophyll. This style-like projection beyond the broader base of the sporophyll still exhibits a conduplicate structure in transverse sections and retains its stigmatic margins. It should be noted in this connection that the styles of the Magnoliaceae likewise exhibit a conduplicate structure.

The free dorsal surfaces of the carpels of *Himantandra* are coated below the level of the style with numerous dark brown peltate scales (*figs. 4, 7, 11, 13, 14*). The abaxial parts of the carpels contain more or less numerous nests of sclereids, such as occur in the tissue of the torus (*fig. 7*). Spherical secretory cells are of common occurrence in the carpels, as in other parts of the flower. The level of attachment and the orientation of the large, much flattened, anatropous ovule fluctuate considerably from carpel to carpel and from flower to flower of different collections of *H. Belgraveana*. Thus, the ovule may be attached at a higher level where the carpel is open (*fig. 4*), or at a lower one where the carpel is adnate to the torus.

The vascular system in the cone-shaped, carpel-bearing, apical part of the torus is simple in contrast to its complexity in subtending regions. The vascular strands remaining after departure of traces to fertile and sterile microsporophylls briefly reassemble at the top of the columnar part of the torus into a weakly defined cylinder of bundles, most of which are dorsal bundles of carpels. The dorsal traces of all of the carpels, except the 2 or 3 distal ones, enter the megasporophylls without branching. A variable number of bundles (4–8) left in the center of the torus divide in various ways to form two (rarely one) small ventral traces for each of the carpels. The dorsal bundles of the 2 or 3 uppermost carpels arise also from these

central strands, but these dorsals first give off ventral traces to lower carpels of the same orthostichies. The carpel of *Himantandra*, therefore, is a modified 3-veined megasporophyll having a well-developed dorsal vein and two more or less reduced ventral ones. The dorsal vein extends upward as far as the middle or lower third of the style. It is much enlarged for a short distance in the region of the junction of the style and ovary. The ventral veins occasionally terminate in the ovule (especially when one ventral only is present), but usually they continue short distances in the margins of the carpels above the attachment of the ovule (*fig. 14*). However, the ventral veins rarely if ever extend upward into the style.

FRUIT. Soon after anthesis, the styles apparently atrophy and the basal portions of the carpels become increasingly conrescent. The mature fruit is a subglobose or somewhat elongated syncarp, upon the surface of which the outlines of the outermost imbricate carpels can be only indistinctly, if at all, perceived. The whole exterior surface is more or less persistently lepidote. The lower carpels appear shorter than those at the apex of the fruit, the constituent carpels being irregular in shape and apparently often distorted by mutual pressure. The original conical apical portion of the torus elongates, carrying the distal carpels upward and thus somewhat distorting the spiral arrangement. Sometimes the carpels are 2- or 3-ranked and strictly superposed.

All of the fruits available to us are dried, in which condition they are hard and coriaceous; according to Diels (5: 129) they are fleshy when fresh and somewhat suggestive of the syncarps of *Annona*. The inner walls of the carpels thicken after anthesis and in dried fruits form coriaceous dissepiments. During development of the fruit the carpels are apparently under lateral pressure, and the locules eventually appear as mere slits, much narrower in proportion than they are in the flower (*fig. 7*). The seeds, in all specimens examined by us, are solitary, greatly flattened, submembranous and suborbicular. In dried material we have not been able to perceive whether such seeds are fertile, and for the present we can neither add to nor verify Diels' statements (5: 130).

RELATIONSHIPS OF THE HIMANTANDRACEAE. In studying the relationships of families, it is essential to weigh evidence from all organs and parts of the plants. In the past, excessive emphasis has not infrequently been placed upon similarities between one or two morphological features without regard to outstanding differences in other parts of the plants, or conversely to stress differences in one organ or tissue without allowing for similarities in other organs or tissues. It should be noted in this connection that certain of the morphological similarities within the Ranales appear to be due to retentions of structures that characterized the primitive ranalian stock, whereas others represent parallel specializations from a common ancestry. Thus, the retention of vesselless xylem, in itself, does not provide adequate evidence for combining *Trochodendron*, *Tetracentron*, and the Winteraceae in an independent order, viz. Homoxylées of van Tieghem (9). Nor are the specialized calyptrate structures of *Drimys*,

Eupomatia, and *Himantandra* necessarily indicative of close relationship. Furthermore, certain superficial similarities or differences between specific organs prove to have been misleading when the ontogeny and the internal structure of these organs are carefully investigated.

There are numerous similarities between the Degeneriaceae, Magnoliaceae, and Himantandraceae. Many of these similarities (e. g. presence of spherical secretory cells, sclerenchymatous medullary diaphragms, stratified phloem, wood fibers with small bordered pits, superficial origin of periderm, monocolpate pollen, stomata with subsidiary cells oriented parallel to the guard cells, etc.), taken independently, are not necessarily indicative of close relationships, since they occur in other representatives of the Ranales. However, the *totality* of the similarities does indicate that the three families are more closely related to one another than to other ranalian families. In fact, the three families form a compact group within the Ranales comparable to that composed of the Monimiaceae, Lauraceae, Gomortegaceae, and Hernandiaceae.

The structure of the stem, including the cortex, pith, and vascular tissues, is of a basically similar type in the Degeneriaceae, Magnoliaceae, and Himantandraceae, and differs markedly from that which occurs in other ranalian families, with the possible exception of the Annonaceae. The wood of *Degeneria* is of a comparatively primitive type, whereas that of *Himantandra*, with its transitions to porous perforations and alternate lateral pitting of the vessels, is obviously more highly specialized. The woods of the numerous representatives of the Magnoliaceae provide a graded series of transitions between these structural extremes. However, the range of morphological variability of the stem is no greater than in single families or even genera of the dicotyledons and therefore, by itself, does not provide cogent arguments for differentiating the plants into three families or even for excluding them from close relationship to the Annonaceae.

The vascularization of the leaf in the Degeneriaceae, Magnoliaceae, and Himantandraceae is of a characteristic and basically similar type and serves to differentiate the three families from other ranalian families (including the Annonaceae) which have secretory cells and monocolpate pollen. Throughout the Magnoliaceae the vascularization of the foliar organs is complicated by the presence of stipules and provides a reliable means for differentiating the vegetative shoots of magnoliaceous plants from those of *Degeneria* and *Himantandra*. The peltate scales, crystalliferous parenchyma, and peculiar stomatal arrangements of *Himantandra* differentiate its vegetative organs from those of *Degeneria* and the Magnoliaceae. It should be admitted, however, that such differences in the vegetative organs, by themselves, do not afford a thoroughly reliable argument for segregating the plants into separate families rather than into tribes of a single family. Only when combined with outstanding differences in the reproductive organs is there a summation of evidence in favor of separate families.

The flowers of *Degeneria* and *Himantandra*, as of *Michelia* and *Elmer-*

rillia, are borne at the apex of axillary shoots. These shoots, as the terminal flowering ones of *Magnolia* and *Liriodendron*, are essentially vegetative, since they exhibit various stages in the reduction of typical leaves to scales (*Himantandra*) or to stipular bud-scales (Magnoliaceae). The flowers of *Degeneria* and *Himantandra* have clearly differentiated pedicels, whereas those of the Magnoliaceae are sessile on the last vegetative node. The flowers of *Degeneria* are provided with distinct sepals and petals, those of *Himantandra* with a calyptrate corolla enclosed within a calyptrate calyx, and those of the Magnoliaceae with tepals or subsimilar sepals and petals. The tepals of the Magnoliaceae usually have a conspicuously petaloid texture and internal structure, whereas the homologous parts of *Degeneria* and *Himantandra* are coriaceous and provided with very numerous nests of sclereids. The immature flowers of the latter genera are not enclosed within a bud, whereas those of the Magnoliaceae are enveloped within one or more pairs of stipular bud-scales.

There are no staminodes in the flowers of Magnoliaceae, whereas *Degeneria* has numerous inner staminodes and *Himantandra* both inner and outer ones. The microsporophylls of *Degeneria* and *Himantandra* are not differentiated into filament, anther, and connective, and their sporangia are immersed beneath the abaxial surface of the sporophyll. On the contrary, the microsporophylls of the Magnoliaceae are typical stamens with conspicuous protuberant anthers, but they tend to retain the 3-veined type of vascularization that characterizes both the fertile and sterile sporophylls of *Degeneria* and *Himantandra*.

The floral axis of the Degeneriaceae and Himantandraceae, unlike that of most Magnoliaceae, is short, and the torus is characterized by having a conspicuous concavity. In *Himantandra* the cone-shaped, carpel-bearing apex of the torus projects beyond this concavity, whereas in *Degeneria* the solitary carpel is attached within it. In the latter genus, the carpel is a 3-veined, conduplicate megasporophyll of relatively unmodified form, bearing numerous ovules on its morphologically adaxial surface. The attachment of the ovules is remote from the free stigmatic margins of the sporophyll. The numerous (rarely reduced to two, e. g. *Pachylarnax*) carpels of *Himantandra* and the Magnoliaceae have well-differentiated styles, which are plume-like in *Himantandra* and commonly provided with more or less decurrent stigmatic surfaces in Magnoliaceae. As contrasted with *Degeneria*, the ovules are reduced in number, commonly to one in *Himantandra* or to two in many representatives of the Magnoliaceae. Such morphological divergences are impressive, but a detailed study of the carpels of *Himantandra* indicates that they probably represent specializations of the 3-veined, conduplicate type of carpel encountered in *Degeneria*. With reduction in the number of ovules to one or a few more or less basally attached ones, there appears to have been a concomitant narrowing of the upper sterilized part of the conduplicate megasporophyll, forming styles which retain a conduplicate structure and stigmatic margins. Reduction of the "decurrent" stigmatic surfaces in certain of the Magnoliaceae

leads to the formation of a style with a nearly apical stigmatic surface. In *Himantandra*, as in many Magnoliaceae, there is more or less adnation and concrescence of carpels both preceding and following anthesis. In *Degeneria*, part of the maturing seeds are attached by slender much elongated funicles, suggestive of the suspended seeds of certain Magnoliaceae. The pollen of the Degeneriaceae, Magnoliaceae, and Himantandraceae is of a similar monocolpate type, that of *Himantandra* more closely resembling the pollen of certain Magnoliaceae than of *Degeneria*.

Outstanding differences in the carpel, calyx, and corolla render difficult the inclusion of *Degeneria* and *Himantandra* in a single family, in spite of obvious similarities in the form of the floral axis, the stamens, and the staminodes. Furthermore, numerous floral differences form a serious obstacle to including these genera in the Magnoliaceae. Aside from certain similarities in the pollen, in the vascularization of the stamens, and in the carpels of *Himantandra*, there is scant floral evidence for inferring close relationship to the Magnoliaceae. Such evidence is amply provided, however, by the vegetative organs. Thus, the summation of evidence from both vegetative and reproductive organs indicates that in the Degeneriaceae, Himantandraceae, and Magnoliaceae we are concerned with three distinct but closely related families. As will be shown in subsequent papers, similar summations of evidence indicate that such ranalian plants as the Winteraceae, *Illicium*, the Schizandraceae, and *Tetracentron* are only remotely related to this compact group of three families. To include them within the Magnoliaceae, as some investigators have done, broadens this family even beyond the limits of a natural sub-order.

PRINCIPAL LITERATURE CITED

1. BAILEY, I. W., and A. C. SMITH. Degeneriaceae, a new family of flowering plants from Fiji. Jour. Arnold Arb. **23**: 356-365. *pl.* 1-5. 1942.
2. BAKER, E. G. Himantandraceae (of Dr. H. O. Forbes's New Guinea Plants). Jour. Bot. **61**: Suppl. 2-3. 1923.
3. DIELS, L. Ueber primitive Ranales der australischen Flora. Bot. Jahrb. **48**: Beibl. **107**: 7-13. 1912.
4. ——— Die Anonaceen von Papuasien. Bot. Jahrb. **49**: 113-167 (*Himantandra*, pp. 164-165. *f.* 6). 1912.
5. ——— Ueber die Gattung Himantandra, ihre Verbreitung und ihre systematische Stellung. Bot. Jahrb. **55**: 126-134. *f.* 1. 1917.
6. McLAUGHLIN, R. P. Systematic anatomy of the woods of the Magnoliales. Trop. Woods **34**: 3-39. 1933.
7. SMITH, A. C. A nomenclatural note on the Himantandraceae. Jour. Arnold Arb. **23**: 366-368. 1942.
8. SPRAGUE, T. A. Galbulimima baccata F. M. Bailey. Hook. Ic. Pl. **31**: *pl.* 3001. 1915.
9. TIEGHEM, P. VAN. Sur les dicotylédones du groupe des Homoxylées. Jour. de Bot. **14**: 259-297, 330-361. 1900.

EXPLANATION OF PLATES

All plates illustrate *Himantandra Belgraveana* (F. v. Muell.) F. v. Muell. The figures are photographed from or drawn from various specimens, these being indicated in each case.

PLATE I

FIG. 1. *Clemens 6584a*. Dorsal surface of partially cleared leaf, showing peltate scales and crystal-bearing cells of the epidermis, $\times 260$. FIG. 2. *Brass & Versteegh 11195*. Lower epidermis of fully cleared leaf, showing circular clusters of stomata, $\times 260$.

PLATE II

FIG. 3. *Clemens 5538*. Transverse section of young conduplicate leaf, $\times 34$. FIG. 4. *Clemens 11100*. Transverse section of flower above the level of adnation of the conduplicate carpels, showing free stigmatic margins and the attachment of an ovule, $\times 100$. FIG. 5. *Brass & Versteegh 11195*. Transverse section of a fertile microsporophyll, showing embedded sporangia and four short arcs of endothecia, $\times 100$.

PLATE III

FIG. 6. *Clemens 3678*. Transverse section of immature flower, showing open conduplicate carpels, $\times 37$. FIG. 7. *Brass & Versteegh 11195*. Transverse section of older flower, showing adnation and coalescence of carpels, $\times 37$.

PLATE IV

FIG. 8. *Ledermann 10884a*. Transverse section of basal part of the midrib, showing foliar vascular dictyostele, $\times 50$. FIG. 9. *Y. U. 15717*. Transverse section of secondary xylem from a large stem, $\times 50$. FIG. 10. *Y. U. 15717*. Tangential longitudinal section of the same piece of wood, $\times 50$.

PLATE V

FIG. 11. *Brass 12103*. Flower with calyptrate calyx, calyptrate corolla, staminodes and stamens removed, approx. $\times 10$. FIG. 12. Half of same flower as in *fig. 11*, viewed from cut surface, showing shape of torus and attached lower and distal carpels, approx. $\times 10$. FIG. 13. *Clemens 3586*. Carpel with short and comparatively smooth style, approx. $\times 15$. FIG. 14. Carpel from flower of *fig. 11*, showing plumose style, position of ovule (micropyle, *micr.*), ventral bundle, *ven. bn.*, and ovule trace, *ov. tr.*, approx. $\times 15$.

PLATE VI

FIGS. 15-23. Diagrams of successive segments through flowering shoot and base of torus, showing average or basic vascular condition in *Himantandra*. Lower bract traces, *lo. br. trs.*; upper bract traces, *up. br. trs.*; bud trace, *bu. tr.*; cortical bundles, *cor. bn.*; outer calyptra, *o. cal.*; inner calyptra, *in. cal.* FIG. 24. *Brass 12572*. Outer staminode, approx. $\times 6$. FIG. 25. *Brass 12572*. Stamen, approx. $\times 6$. FIG. 26. *Brass 12572*. Inner staminode, approx. $\times 6$.

BIOLOGICAL LABORATORIES AND ARNOLD ARBORETUM,
HARVARD UNIVERSITY.